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Social discounting involves modulation of neural value signals by temporo-parietal junction

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Contributions

- Designed research: TS, BW, PK, PNT, TK
- Performed research: TS
- Analyzed data: TS
- Wrote the paper: TS, BW, ZH, PK, IIK, PNT, TK

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Abstract

Most people are generous, but not towards everyone alike: generosity usually declines with social distance between individuals, a phenomenon called social discounting. Despite the pervasiveness of social discounting, social distance between actors has been surprisingly neglected in economic theory and neuroscientific research. We used fMRI to study the neural basis of this process to understand the neural underpinnings of social decision making. Participants chose between selfish and generous alternatives, yielding either a large reward for the participant alone, or smaller rewards for the participant and another individual at a particular social distance. We found that generous choices engaged the temporo-parietal junction (TPJ). In particular, the TPJ activity was scaled to the social-distance-dependent conflict between selfish and generous motives during prosocial choice, consistent with ideas that the TPJ promotes generosity by facilitating overcoming egoism bias. Based on functional coupling data we propose and provide evidence for a biologically plausible neural model according to which the TPJ supports social discounting by modulating basic neural value signals in the ventromedial prefrontal cortex to incorporate social-distance-dependent other-regarding preferences into an otherwise exclusively own-reward value representation.

Significance Statement

People often consider the well-being of others. However, they are more likely to be generous towards individuals they feel close to than to those they only meet sporadically. Using neuroimaging tools, we show that the decline in generosity across social distance is realized by the interplay of two brain structures – the ventromedial prefrontal cortex coding the relative appeal of a selfish or a generous option, and the temporo-parietal junction modulating appeal signals of the generous outcome, depending on social distance between participant and beneficiary. Based on these findings, we developed a biologically plausible model explaining social discounting in particular, and prosocial behavior in general. Our study opens up new avenues to understand and tackle frictions arising in social networks.

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Introduction

Prosociality is one of the most fundamental qualities of all human societies. Without the ability to take other people's interests into account human relationships would disintegrate and societies would malfunction. It has been widely demonstrated in laboratory and field experiments that individuals consider the welfare of others in their decisions and the consequences a decision has on them (1-3). Although almost all of us behave prosocially at times, it is clear that people are not equally generous to everyone alike. Rather, generosity decreases as a function of the closeness of the relationship between two individuals (2, 4). However, it is currently unknown how social distance contributes to the decision process on a neural level. In the present study we set out to address this question.

Our first aim was to investigate the systematic influence of social-distance dependent levels of generosity on neural activation. This was investigated using a social discounting experiment adapted to the functional magnetic resonance imaging (fMRI) environment (1). We measured blood oxygen-level dependent (BOLD) responses while subjects made choices between selfish and generous rewards for themselves and for other people that varied in social distance. Choosing selfishly yielded a payoff only for the subject, while making a generous choice resulted in a lower payoff for the subject coupled with a reward for another person at a specific social distance (fig. 1). Next, based on the individual choices, we reconstructed the social-distance-dependent other-regarding utility (ORU), that is, the value participants attached to increasing the wealth of another person at a given social distance.

We then asked which brain regions showed activity that correlated with the difference between other- and self-regarding utilities. Our paradigm was designed so that the degree of generosity varied systematically as a function of social distance while objective economic outcome parameters – own- and other-person payoffs – were kept constant. This allowed us to identify the neural correlates of social-distance-dependent other-regarding preferences independent of objective payoffs.

We hypothesized, based on existing literature (5-10), that own reward values are represented in the brain's valuation system, specifically in the ventromedial prefrontal cortex (VMPFC). Furthermore, changes in other-regarding value would recruit areas associated with theory of mind (ToM) and altruistic choice, such as the temporoparietal junction (TPJ) (11, 12). Should this be the case, this would show that social distance is indeed systematically integrated into the neural underpinnings of the decision process.

Our second aim was to investigate the role of the TPJ in prosocial behavior in more detail. To this end, we tested the predictions of two competing ideas on the role of the TPJ during prosocial choice in general, and social discounting in particular. Previous research showed that this region is involved in tasks requiring the ability to represent and understand others' perspectives (12, 13) and in social and selfish decisions (14-17). Thus, the TPJ's implication in prosocial choice, perspective-taking, empathizing and ToM suggests that it plays a role in putting oneself in someone else's shoes. In other words, the TPJ may encode the other-regarding value participants attach to increasing the well-being of another person. Individuals empathize more with people they feel close to than with more distant others. Therefore, if this hypothesis is true, TPJ activation should correlate positively with the social-distance-dependent ORU. This view of the role of the TPJ is challenged by more recent studies postulating that TPJ activation solves the conflict between generous and selfish motives (16). According to this hypothesis, to make a generous decision, the putatively natural bias to maximize own-payoff needs to be overcome (18). If the TPJ enables overcoming egoism bias, activation should be high when the temptation to be selfish is high (i.e. large social distance and/or large selfish reward) and low when there is little conflict between selfish and generous motives (i.e. small social distance and/or relatively small selfish reward).

Our results confirmed the latter hypothesis according to which the TPJ plays a role in overcoming the default response of maximizing one's own profit and thus behaving selfishly, rather than in representing other-regarding value. We also asked how the brain implements generous decisions. Specifically, we propose that the TPJ facilitates generous decisions by modulating basic reward signals in the VMPFC, incorporating other-regarding preference signals into an otherwise exclusive own-reward value representation, thus computing the subjective value for a social reward. Thus, the TPJ supports prosocial choice by shaping neural value signals in the VMPFC whenever the

temptation to be selfish needs to be overcome; the stronger the temptation to be selfish, the more the TPJ upregulates VMPFC activity in favor of generous choices.

A mechanistic model that integrates these data makes two predictions for which we provide empirical support: first, VMPFC activity should be higher during generous than selfish decisions. Second, connectivity between the TPJ and the VMPFC should be stronger during generous than during selfish decisions. Together, our findings suggest that prosocial decisions arise from a refined interplay between the VMPFC and the TPJ. In particular, value signals in the VMPFC are orchestrated by the TPJ according to the social distance between the decision maker and the recipient of generous decisions.

Results

Behavioral results

We inferred social discounting parameters based on the participants' individual choices, and used the obtained social discount functions to econometrically reconstruct the social-distance-dependent ORU for each individual (1). To this end, we first determined, for each social distance level, the point at which a participant was indifferent between the selfish (yielding a larger reward for the participant) and the generous alternative (yielding a smaller reward for the participant plus a reward for the other person) using logistic regression. The difference in reward magnitudes for the participant between the two alternatives at the indifference points represented the amount of money a subject was willing to forego to increase the wealth of another person at a given social distance, and could be construed as a social premium equivalent to the utility of increasing the other person's well-being. For example, if a participant was indifferent between €125 own-reward and €75 own-reward and €75 for a person at social distance 1, this participant was willing to forego €50 (the social premium) to increase the wealth of the other person by €75. Subsequently, we fit a standard hyperbolic model (2) (see methods) to the individual social-distance-dependent social premiums with the parameters k ($Mdn=0.078$) and V ($Mdn=74.15$). As expected, the magnitude of the social premium subjects were willing to pay for someone else's benefit declined with increasing social distance. The standard hyperbolic model captured the individual

discounting behavior well (mean $r^2=0.72$, $SD=0.242$; fig. 2 shows the median social premiums together with the best-fitting hyperbolic function).

These findings replicated those of previous studies on social discounting (1, 2) suggesting that the scanner environment did not substantially affect discounting behavior compared to studies carried out in more natural surroundings. The obtained individual hyperbolic fits served as estimates of the decline in other-regarding value across social distance, and were used to estimate the individual ORUs, which corresponded to the hyperbolic fit plus the sure €75 (constant, within-subject) for the participant herself.

Neural mechanisms of social discounting

Social discounting is the consequence of the social-distance-dependent balance between generous and selfish motives

The fundamental premise in our study is that, in essence, a prosocial decision results from the balance between generous and selfish motives. Due to social discounting, the balance between generous and selfish motives is increasingly tilted towards selfishness as social distance increases. With this premise in mind, we tested the hypothesis that the TPJ is involved in orchestrating the balance between generous and selfish motives across social distance. We also hypothesized that the TPJ would perform this function together with classical value coding regions such as the VMPFC (8, 19).

Neural value signals in the valuation network

First, we investigated the neural correlates of selfish rewards. To identify brain regions associated with own-reward value coding, we examined neural activity during the decision period of selfish decisions only. For this analysis we concentrated on the VMPFC, and asked whether BOLD activity in the VMPFC covaried with selfish reward magnitude, thus with the value of the selfish decision. We used a region of interest (ROI) based on a meta-analysis $[-2, 40, -4]$ (20), that suggests this part of the VMPFC plays a

role in value processing. Using a 6 mm sphere around the ROI, we found significant correlations within the VMPFC (-6, 41, -5; $t_{(22)}=3.10$, $p=0.017$, small volume (SV) family-wise error (FWE) corrected, SI Appendix, fig. S3, table S1).

Next, we also included generous decisions in our analysis. Interestingly, we found that activity in the VMPFC was significantly higher during generous than during selfish choices (0, 47, -20; $t_{(22)}=4.21$, $p=0.028$, whole brain FWE corrected; fig. 3A, SI Appendix, table S2). Thus, in line with other findings (21), the VMPFC coded not only the own-reward value of a selfish choice, but also generosity in addition to own-reward value, possibly reflecting the satisfaction derived from increasing someone else's wealth (21). Generous decisions also elicited stronger responses than selfish decisions in the right (60, -58, 31; $t_{(22)}=5.15$, $p<0.001$, whole brain FWE corrected; SI Appendix, table S2) and left TPJ (-24, -79, 52, $t_{(22)}=4.51$, $p=0.002$, whole brain FWE corrected). This section of TPJ has previously been shown to be associated with ToM and altruistic choice (11). We used these brain areas as ROIs in all subsequent analyses to further characterize their contribution to social discounting.

Generous decisions recruit the TPJ to resist the temptation to be selfish

Our design allowed us to shed light on two competing hypotheses about the role of the TPJ in social decision-making. If the TPJ was important for encoding the social-distance-dependent value participants derive from increasing someone else's well-being, we would expect a positive correlation between TPJ activity and the ORU. To test the first hypothesis, we searched for brain regions whose activity correlated with the social-distance-dependent other-regarding value, using the individual ORUs as parametric regressors at decision onset. Inconsistent with our predictions, the parametric analysis revealed no activation in the TPJ, even at very liberal thresholds ($p<0.1$, uncorrected; see supplemental material for more analyses; SI Appendix, table S3).

Next, we tested the second hypothesis, that the TPJ is associated with overcoming egoism-bias. We reasoned that the temptation to make a selfish choice should be stronger, the larger the utility of the own reward relative to the social-distance-dependent other-regarding utility. By extension, the stronger the temptation to be

selfish, the more effort should have been exerted in order to overcome this temptation when a generous decision had been taken. Thus, we hypothesized that activity in brain regions important for overcoming egoism bias would scale to the difference between own-reward and other-regarding values when a generous choice is revealed. We therefore searched for BOLD signals that correlated with the difference between own-reward and other-regarding values during generous decisions. This analysis revealed, among others, activation in the right parietal cortex, expanding into the parietal part of the TPJ (rTPJ; 42, -79, 46; $t_{(22)}=5.55$, $p=0.019$, whole brain FWE corrected; SI Appendix, table S4). A conjunction analysis, revealing the strict intersection between this contrast and the contrast yielding generosity-related activations confirmed that this was indeed the same region as the one engaged during generous decision making. Additionally, a ROI-analysis using a mask for the parietal subsection of rTPJ (22), an area known to be involved in social cognition, confirmed that it was activity in this ‘social’ part of the TPJ that correlated with the parametric modulation of the temptation to be selfish during generous decisions ($p=0.032$, SV FWE corrected, fig 3B).

Importantly, according to the second hypothesis, the rTPJ should be active when the conflict between selfishness and generosity is resolved in favor of the latter (i.e. in generous choices), while activity should be less when selfish choices are made. In support of this idea, rTPJ activation survived when contrasting the difference in own-reward and ORU during generous against selfish decisions, suggesting that the rTPJ was more active during generous (i.e., when the temptation to be selfish had been overcome) than during selfish choices (42, -79, 46; $t_{(22)}=7.10$, $p<0.001$, whole brain FWE corrected; SI Appendix, table S5). Thus, rTPJ activation correlated with the difference between own reward values and ORU when generous choices were made, but not with ORU in general, irrespective of the actual decisions taken. Although the lack of evidence in favor of the first hypothesis of TPJ function is not evidence against ToM, it is worth noting that rTPJ activity was in fact *positively* correlated with the difference between own-reward and other-regarding value. In other words, rTPJ activity was *negatively* correlated with other-regarding utility alone, which is difficult to reconcile with the ToM-based hypothesis. Conversely, our results are in line with the hypothesis of overcoming egoism bias, and are therefore more consistent with the idea that the rTPJ facilitates generous choice whenever a conflict between egoistic and selfish motives needs to be resolved.

The TPJ was functionally connected with the VMPFC when egoism bias was overcome

So far, our data have shown that the VMPFC encoded the value of own-reward during selfish decisions, and both the VMPFC and the TPJ were more engaged during generous than during selfish choices. Furthermore, the rTPJ activation pattern was consistent with the idea that the rTPJ facilitates prosocial choice by overcoming the temptation to maximize own payoff. We next asked how a social-distance-dependent prosocial choice is implemented in the brain. We propose a model of generous choice according to which the VMPFC encodes goal values. We hypothesize that the TPJ suppresses egoism bias by modulating basic value signals in the VMPFC to incorporate other-regarding preferences into an otherwise exclusively own reward value representation.

If our hypothesis was true, functional connectivity between the rTPJ and the VMPFC should be higher during generous than during selfish decisions. Our idea was inspired by recent models of self-control (8, 22) according to which basic value representations in the VMPFC are modulated by superordinate brain regions encoding higher-order considerations, such as long-term goals or other-regarding preferences. Thereby, these higher-order factors are incorporated into basic valuation signals of the VMPFC. Adapting this approach to social decision-making, we propose that the rTPJ modulates activation in the valuation network and orchestrates social decision-making in favor of other-regarding instead of individual preferences.

To test the hypothesis, we conducted a psychophysiological interaction analysis (PPI) to identify which brain regions were functionally more strongly connected with the rTPJ during generous than during selfish decisions. To this end, we placed a seed (fig 4A) in the individual peak activations in the right TPJ cluster associated with overcoming egoism bias. The PPI analysis identified functional connectivity between the rTPJ and the VMPFC ($t_{(14)} = 6.61$, $p = 0.031$, whole-brain FWE corrected; fig. 4B, SI Appendix, table S6). A conjunction analysis confirmed that the activated VMPFC cluster was indeed the same region as the VMPFC ROI that coded own-reward value during selfish decisions. Thus, compared to selfish decisions, the TPJ increased functional connectivity with regions associated with own-reward processing during generous decisions.

Discussion

In order to function well in our society it is important to share resources with others. The closer our interaction partners are to us, the more likely we are to be generous towards them. Thus, the social context in which a decision is made strongly affects how the information is processed, making it essential for our brain to be able to encode such social context factors (23). However, neuroeconomic theories have so far neglected social distance in models of decision-making. The current experiment investigated the neural correlates of social discounting and aimed to provide support for a neural model of social distance-dependent generous decision-making. Generosity requires overcoming egoistic motives (1, 2, 16, 24), and the temptation to be selfish grows with increasing own-reward magnitude, but also with increasing social distance. We were able to demonstrate, that a region associated with ToM, social cognition and decision making, the TPJ, is involved in this process (24). However, contrary to the predictions of the first, ToM-based, hypothesis we find no evidence that the TPJ computes other-regarding value. Instead, we propose that the TPJ facilitates overcoming egoistic motives to maximize own-payoff during generous decisions by modulating basic value signals in the VMPFC through integrating other-regarding preferences into an otherwise exclusively own-reward value representation (24, 25). Thus, the stronger the social-distance-dependent temptation to be selfish, the more the TPJ is engaged and VMPFC-value signals become upregulated to facilitate a generous decision.

On a behavioral level, we replicated existing findings on social discounting, confirming that generosity declines hyperbolically across social distance, with individuals being more willing to forego a reward for recipients at close social distances. Hyperbolic social discounting has been observed in diverse locations, populations, cultures as well as under different experimental conditions and with various methods of implementing social distance and eliciting social preferences (1, 2, 26-28). This suggests that a hyperbolic discount function is an accurate, valid and useful description of social discounting behavior, even though it is likely that there is a large range of individual motives underlying the actual decisions during social discounting.

To reveal the neural mechanisms underlying social discounting, we first identified regions that code value signals. When participants made selfish choices, activity in the

VMPFC reflected own-reward value, replicating findings on valuation processes from a multitude of studies (5, 7-9, 29). Additionally, we found that the VMPFC was more active during generous than during selfish choices, even though selfish decisions yielded higher payoffs for the participants. This is in line with studies which postulated that VMPFC activity represents the extra value obtained from charitable giving (21). Thus, it is likely that the increased activation during generous choices reflected the additional satisfaction derived from sharing a reward during generous decision-making.

Our results suggest that the TPJ is important for overriding selfish impulses during prosocial decisions. Note that recent research on TPJ function suggests that it is not a monolithic structure that supports one single cognitive function, but is more likely to be composed of anatomically and functionally distinct subdivisions that may subserve different computational roles such as value, salience and ToM (11, 24, 25, 30, 31). Although we cannot rule out that our subjects used ToM or other mechanisms to make their decisions, it is possible that we found no evidence in favor of the first, ToM-based hypothesis simply because we did not explicitly elicit ToM-cognition. Thus, we are not rejecting the wealth of evidence from previous work relating the TPJ to ToM and mentalizing. Instead, we complement existing literature by lending support to the idea that subparts of the TPJ have the additional role of overcoming egoism bias and thus facilitating prosocial choice. Future research should study the TPJ in more detail and map the putative different cognitive functions to its different subdivisions.

In summary, the present findings provide new insights into social decision making. We were able to characterize the role of the TPJ and proposed a neural model of prosocial choice. Our data identify the TPJ as the core component in overcoming egoism bias. This finding has a significant impact on neuroeconomic theory that has so far neglected the effect of social distance on prosocial decision making. Having shown that social distance is an important component of an individual's decision-making process it should be integrated into future models of decision making. Furthermore, using social discounting to understand the influence of social factors and individual differences in generosity and other-regarding behavior opens up new opportunities to evaluate psychopathologic decision-making and antisocial behavior in more detail.

Materials and Methods

Participants. 27 subjects (mean_{age}=25.03, 14 men) were tested. Participants received a €10 show-up fee and an additional amount depending on their decisions in the experiment (own reward: €7,50 - €16,50, other reward: €2,50 or €7,50), determined by a random draw of one of the trials. All subjects were native German speakers. Participants had no history of psychiatric or neurological disorders. Written consent was obtained according to the Declaration of Helsinki (BMJ 1991; 302: 1194). The study was approved by the ethics committee of the University of Bonn. Subjects were acquired using the subject database of the Life&Brain Centre, University Hospital Bonn.

Stimuli and task. The experimental paradigm was adapted from a cross-cultural study on social discounting (1). During the preparation phase participants received verbal and written instructions for the tasks they carried out during the experiment. Participants started with a self-representation task in which they specified closeness to people in their social environment (1). Using a 20 point scale (1=very close; 20= not close), participants were asked to rate their closeness to the following people: mother, father, siblings, grandparents, family, kin, best friend, circle of friends, colleagues, neighbors, acquaintances, partner, children, and stranger. In case some of these people did not exist in a participant's social environment, the corresponding trial was skipped. This task was aimed at getting subjects used to the idea of social distance and to think about their social network.

In the fMRI scanner, social distance was transformed into a scale consisting of 100 icons (fig. 1). Participants were informed that the purple icon at the left end of the scale represents themselves and the yellow icon stands for a specific person in their social environment. For example, if the yellow icon is directly next to the purple one (social distance 1) this shows the person they feel closest to, e.g. mother or partner. If the yellow icon is at social distance 50 (the middle of the scale) this symbolizes an acquaintance while at social distance 100 it would represent the most socially distant, but emotionally neutral person, such as a stranger. Before entering the scanner, participants were asked to choose and write down names of representatives from their social environment, one for each of the following social distances: 1, 2, 3, 5, 10, and 20. We also included social distance levels 50 and 100 in the experiment, however, as these

distance levels represent remote acquaintances or strangers, subjects were not required to indicate a name. Thus, eight social distances were included. We used a network-based approach, according to which one might mentally assign more than one person to a particular social distance (32). However, in the experiment participants were asked to choose just one person for each distance. The network based approach is important since we assume that an individuals' social network is adaptive and might change within days. For example, bad experience with a friend might result in a readjustment of the perceived social distance to that friend. Furthermore, as negative emotions can interfere with prosocial behavior subjects were explicitly asked to only include individuals they did not have a negative attitude towards (33-35). Subjects did not indicate any problems understanding the scale and the idea of social distance.

In the scanner, subjects were asked to make 160 decisions involving the eight social distances (fig. 1). The task in each trial was to think about the person previously chosen for the specific social distance relevant to the actual trial. Each of the 160 trials started with the presentation of the scale indicating the relevant social distance followed by the generous and selfish options with a mean ISI of 4 sec (jittered: ± 1 sec) and a mean ITI of 6 sec (jittered: ± 1 sec). The temporal and spatial ordering of the selfish and generous option presentation was pseudo-randomized. For the specific social distance, subjects had to choose between these two alternatives. The selfish alternative always yielded a large reward for the participant alone, while the generous option yielded a smaller reward for the participant and an additional reward for the person at the indicated social distance. The selfish reward varied between €75 and €165, changing in increments of €10, resulting in ten selfish alternatives. The generous option was a fixed reward of €75 for the participant and €75 for the other person (high other-reward trials), or, €25 for the other person, respectively (low other-reward trials). The presentation order of social distances, selfish and generous alternatives was fully randomized. Subsequent to the experimental part in the scanner, subjects were asked to name the people they assigned to the specific social distances again, serving as a manipulation check and indicate demographic information.

After completing the last questionnaire, subjects received their payment. In addition to the €10 show-up fee, a randomly chosen trial was paid out. Depending on whether the participant chose the selfish or the generous alternative in that specific trial, she

received 10% of the selfish or the generous reward respectively. The money for the selfish option was paid directly to the participant, and for the generous option subjects were asked to indicate the address of the other person. If the randomly chosen trial was about a person at social distance 50 or 100, a random person on the campus of the University of Düsseldorf, Germany received the reward. Thus, the experiment was fully incentive-compatible, did not include deception and met the experimental standards of behavioral economics.

Social discount function. Since we aimed to quantify the degree of generosity as a function of social distance, we estimated the amount of money a participant was willing to forego in order to benefit a specific other at a given social distance (2). We first determined, for each social distance level, the point at which a participant was indifferent between the selfish and the generous alternatives, using logistic regression as described above. The decision maker switched from being generous to being selfish as selfish rewards increased. If the decision maker switched from generous to selfish decisions between a selfish reward of €135 and €145, the indifference point would be determined to be €140, thus a 50% probability of choosing generous and 50% of choosing selfish. We interpreted the amount foregone (the indifference point minus the €75 the subject would certainly get if he chose the generous option) as a social premium the participant was willing to pay in order to benefit the other. We fit the following standard hyperbolic model to the individual, social-distance-dependent social premiums (2):

$$v = \frac{V}{(1 + kD)}$$

Equation 1: Hyperbolic discount function

where v symbolizes the magnitude of a reward received by another person at social distance D . The parameter V refers to the social premium a subject is willing to pay in exchange for endowing another person with reward v . Thus, V can be interpreted as the socially discounted other-regarding utility of improving the wealth of another individual at social distance D . V is equal to the self-regarding utility at social distance $D=0$, thus the intercept with the y-axis, and determines the height of the social discount function. The degree of discounting is described by the parameter k , which indicates the steepness

and shape of the curve (1, 2). The individual hyperbolic fits were used to estimate individual ORUs.

fMRI data acquisition and preprocessing. Scanning was performed on a 3 Tesla Trio Scanner (Siemens, Erlangen, Germany) using an 8-channel head coil. Functional data were acquired using EPI-sequences with a repetition time (TR) of 2.5 s, an echo time (TE) of 30 ms, and a Flip angle of 90 degrees. Each volume comprised 37 slices acquired in an axial orientation covering all of the brain, including midbrain, but sparing parts of the cerebellum. The presentation of the task and recording of behavioral responses were performed using Presentation® software version 14.9 (Neurobehavioral Systems, Albana, Canada). Subjects saw the experiment via video goggles (Nordic NeuroLab, Bergen, Norway) and gave their responses by response grips (Nordic NeuroLab, Bergen, Norway) using their index fingers of both hands.

Neural data of 23 participants were analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK) software. The results are visualized using the xjview toolbox. Three subjects had to be excluded due to extreme head-movements during the experiment ($> 4\text{mm}$ translation, $> 4^\circ$ rotation). One subject had to be excluded who made exclusively selfish decisions, even when being generous did not involve any reduction in own-reward, as the aim of this study was to investigate pro-social behavior. Indeed, no social discount function can be fit to the data when a participant shows no variation in other-regarding utility.

The following pre-processing steps were carried out: slice timing correction, motion correction, segmentation using the T1 weighted image, linear trend removal, high pass temporal filtering with a filter size of 128 seconds, spatial smoothing using a Gaussian kernel with full-width at half-maximum (FWHM) of 8mm, spatial segmentation and spatial normalization by co-registering the functional with the individual structural data and then transforming it into the Montreal Neurological Institute (MNI) space.

General linear model. We regressed fMRI time series onto two separate general linear models (GLMs). With the first GLM, we aimed to identify brain regions whose activity correlated with selfish reward magnitude and the econometrically reconstructed, social-distance-dependent ORU. In the second GLM, we searched for neural activity correlating

with the relative value, i.e. the social-distance-dependent difference between the selfish value and ORU.

For both GLMs we defined the following five onset regressors: 1) onset of the social distance information at the beginning of each trial, 2) onset of the generous option, 3) onset of the selfish option, 4) onset of the button press when deciding generous, and 5) onset of the button press when deciding selfish. We modeled BOLD responses at these onsets as stick functions. For the first GLM, we used the following three parametric modulators to assess brain activation (36): 1) the social distance level during the onset of the social distance information (onset regressor 1), 2) the econometrically reconstructed ORU, given a generous choice (onset regressor 4), and 3) the selfish reward magnitude given a selfish choice (onset regressor 5). To obtain commensurability, ORU and selfish reward magnitudes were transformed and normalized to a common scale for all analyses.

In the second GLM we used the following parametric modulators: 1) the social distance level during the onset of the social distance information, 2) the difference between own-reward magnitude and ORU, given a generous decision (i.e., the strength of the temptation to choose selfish, given a generous decision; see main text), and 3) the difference between own-reward magnitude and ORU, given a selfish decision. Both GLMs additionally included six movement regressors of no interest, three for translational movements (x, y, z) and three for rotation movements (pitch, roll, yaw). All regressors were convolved with the canonical hemodynamic response function (HRF). For each event, onset regressor parameter estimates were obtained and contrast images of each of the parameters against zero were generated. Furthermore, we obtained contrast images of “deciding generous versus deciding selfish”. The obtained images were transferred to a second level random effects analysis using one-sample t tests on the single-subject contrasts. We performed whole brain corrections for multiple comparisons at the cluster level. For all of the main contrasts reported in the results section and figures, the individual voxel threshold was set to $p > 0.005$ with a minimal cluster extent of $k \geq 10$ voxel (37). Results are reported using the MNI coordinate system.

Psychophysiological Interactions (PPI). We performed a whole-brain PPI analysis with the TPJ as seed region (8, 22, 38). The location of the TPJ seed ROI was based on a 10mm sphere (39) around the peak activation within the conjunction between the contrasts of generous versus selfish decisions (first GLM), and the parametric modulation of the temptation to be selfish (second GLM; 51, -49, 34; rTPJ; fig. 4A). We computed individual average time series within a 4 mm sphere surrounding (39) the individual subject peak activations within the TPJ seed ROI. Seven participants had to be excluded from the PPI analysis because they did not show any individual activation above threshold in the TPJ ROI at $p < 0.05$, uncorrected. This exclusion criterion is the standard for identifying the location of corresponding activations in individual subjects as needed to extract time courses for connectivity analyses (39-42). We created two PPI regressors by computing an interaction regressor between the normalized time-series and the respective condition, i.e. one regressor for generous and one for selfish decisions.

Second, we estimated a GLM with the following regressors: 1) a physiological regressor (i.e., the entire time-series of the seed region over the whole experiment, 2) a psychological regressor for the onset of the generous choices, 3) the PPI regressor for the generous choices, 4) a psychological regressor for the onset of the selfish choices, and 5) a PPI regressor for the selfish choices. The onset and PPI regressors were convolved with a canonical form of the hemodynamic response. The model also included the six motion parameters as regressors of no interest.

In a third step, to identify regions whose connectivity was higher during generous than during selfish choices, single subject contrasts were calculated for the contrast between the PPI regressors, i.e. the contrast between the PPI regressor of the generous compared to the PPI regressor of the selfish choices. Then a second level analysis was performed by calculating a one-sample t -test on the single-subject contrast coefficients. We then identified voxels with significantly higher connectivity difference during generous compared to selfish choices.

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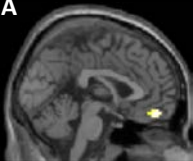
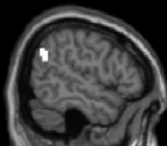
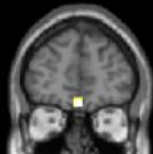
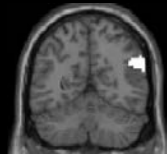
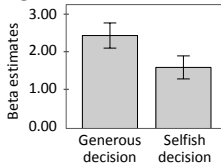
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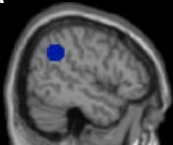
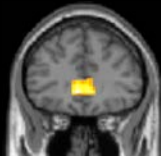
Figure 1: Participants received task relevant information sequentially. First, social distance information was given on a scale consisting of 101 icons (100 icons representing 100 social distance levels plus one icon, shown in purple on the left end, representing the participant himself). The social distance information for a specific trial was indicated by a yellow icon, and additionally, presented numerically as a number on top of the yellow icon (here: social distance 10). Participants chose between a selfish (here: €125 only for themselves) and a generous option (here: €75 for the participant and €75 for a recipient on the specific social distance). The generous and selfish options were then presented sequentially and in random order. All ISI had a mean duration of 4 seconds (jittered by ± 1 sec). Participants indicated their preference during the decision period within a maximum timeframe of 6 seconds. The trials were separated using a fixation cross with a mean ITI of 6 seconds (jittered by ± 1 sec). Note that this figure has been adjusted for illustration purposes; stimulus size and screen format are not to scale with the presentation dimensions used during fMRI scanning. In addition, the figure displays only 21 icons, instead of 101 icons shown during scanning, to facilitate perceptibility.

Figure 2: We determined, for social distance levels 1, 2, 3, 5, 10, 20, 50 and 100, the individual payoff magnitudes at which a participant was indifferent between the selfish (yielding a larger reward for the participant) and the generous alternative (yielding a smaller reward for the participant plus a reward for the other person). The amount foregone, i.e., the difference in own-reward magnitude between the selfish and generous option at indifference point, indicates the willingness to sacrifice a reward to give to another person at a specific social distance. The amount foregone can be interpreted as a social premium that reflects the utility a participant attaches to increasing a recipient's payoff. A standard hyperbolic model was fit to the individual social-distance-dependent amounts foregone to reconstruct the participant's other-regarding utility function. The figure shows the best-fitting hyperbolic function to the median amounts foregone across all participants.

Figure 3: Brain activations during social discounting. (A) BOLD responses in the VMPFC were stronger during generous than during selfish decisions (0, 47, -20; $t(22)=5.47$, $p=0.028$, whole brain FWE corrected; displayed at $p<0.005$, uncorrected, $k\geq 10$ voxel). (B) Generous decisions elicited activation in the posterior part of the rTPJ (mask from Mars et al.(22)) (C) Beta estimates within the rTPJ . The rTPJ was more activated during generous than selfish decisions. (D) Activity in the rTPJ was more strongly modulated by the temptation to be selfish during generous than selfish decisions. Error bars indicate ± 1 SE.

Figure 4: (A) ROI in the rTPJ (51, -49, 34, 10mm sphere) as the seed region for the PPI. (B) Positive functional connectivity of the rTPJ with VMPFC during generous decisions. The PPI analysis revealed that connectivity between the VMPFC and the rTPJ was stronger during prosocial than selfish choices ($t_{(14)}= 6.61$, $p = 0.031$, whole-brain FWE corrected; displayed at $p<0.005$, uncorrected, $k\geq 10$ voxel).

A $x = 0$ **B** $x = 54$  $y = 47$  $y = -56$ **C****D**

A $x = 51$ **B** $x = -6$  $y = 32$

